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Contribution of main stem and tillers to durum wheat (*Triticum turgidum L. var. durum*) grain yield and its components grown in Mediterranean environments

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Abstract

Under terminal drought conditions, cereal varieties with limited tillering have been suggested to be advantageous, because they have fewer nonproductive tillers, thereby limiting water consumption prior to anthesis. In this study, four field trials were conducted over two growing seasons in southern Spain, under rainfed and irrigated conditions. Twenty-five genotypes were studied to evaluate the contribution of the main stem (MS) and tillers to grain yield and its components. Significant differences were found among genotypes for these contributions under non-stressed environments, but these differences were not significant under water-stress conditions. The contribution of the MS to plant grain yield was higher than that of tillers (68% *vs*. 32%) and was stable between years in irrigated trials. However, in the rainfed trials, MS contributed differently depending on year-to-year climate variations. Thus, under favorable weather conditions the contribution of MS to grain yield was higher than in the unfavorable year (85% *vs*. 59%). In irrigated environments, MS and tiller grain yield depended on the number of grains per spike, spikelets per spike, and thousand kernel weight (TKW). Under water-limited conditions, MS yield depended on the number of grains per spike and grains per spikelet, whereas the number of spikelets and TKW had less influence on MS grain yield. Furthermore, under water-stress conditions, high tillering genotypes showed yield levels similar to the genotypes with restricted tillering. Additionally, there was no significant evidence of a positive or negative effect of maximum tiller number on grain yield under rainfed conditions.

Keywords: Uniculm ideotype; Breeding; Crop yield; Durum wheat; Mediterranean environment

1. Introduction

Genotype, agronomic practices, and environmental conditions interact to determine the yield of a crop. Among environmental variables, water stress is one of the major limiting factors of yield in Mediterranean regions (Bennet et al., 1998), especially under rainfed conditions (Loss and Siddique, 1994; Royo et al., 1998). This could be illustrated by the large variation of grain yield observed in such environments. Thus, in 2005, a severely dry year, the average production of durum wheat in Spain was 840 kg/ha, whereas in the previous year, characterized by more favorable conditions, the average production exceeded 2900 kg/ha (AETC, 2005). This high yield variability needs to be managed in order to minimize economic losses in Mediterranean regions, affected by the severity and irregularity of water stress and high temperatures.

Donald (1968) proposed that a uniculm plant of wheat could be more appropriate than freely tillering varieties for well-watered crops with high nutrient inputs. Under Mediterranean conditions of limited water supply, when genotypes with high tillering capacity are used at low density, grain yield is not usually reduced, because plants can produce more tillers than in high crop density, thus potentially compensating for grain-yield losses. However, if the genotypes used do not possess sufficient tillering capacity, low crop density cannot be offset, resulting in a reduced number of spikes per square meter and consequently lower grain yields (Destro et al., 2001). Variation in grain yield also depends on genotype and agricultural management, the

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manipulation of plant density being one of the cropping practices that could exert great impact on grain yield (Leakey, 1971; Baker and Briggs, 1982). In this context, plant density is of particular importance in maximizing yield, since it can play a complementary role. Genotypes with good tillering capacity should be used at low plant density and conversely genotypes with low tillering capacity should be complemented with high plant density to produce an optimum number of competitive plants. Seeding rates vary greatly among regions according to sowing date (Spink et al., 2000), climatic conditions, especially rainfall distribution (Wilson and Swanson, 1962), soil type (del Cima et al., 2004), and cultivars (Anderson and Barclay, 1991). The relationship between grain yield and seed density depends on the proportion of sown seed that results in the establishment of vigorous plants. Most reported research shows that yield increases to a plateau value dependent on the environmental conditions during crop growth (Anderson, 1986). The best rate is that which maximizes yield, and increasing seeding once maximum yield is reached does not improve crop yield (van Herwaarden et al., 2003). The selection of adequate genotypes for a specific environment and good crop husbandry are, therefore, of paramount importance for maximizing yield.

Studies vary in identifying the best genotype. The uniculm ideotype proposed by Donald (1968) stimulated research on detillering experiments in barley (Jones and Kirby, 1977; Kirby and Jones, 1977), in wheat (Islam and Sedgley, 1981), as well as in wheat and barley (Winward et al., 1983). The main conclusion of these studies was that the presence of nonsurviving tillers reduces grain yield under conditions where water is a limiting factor. Recently, Duggan et al. (2005) concluded from an experiment on spring wheat that the cultivars containing a recessive gene for tiller inhibition performed better than the standard tillering cultivars under terminal drought. However, the irregularity of climate, especially yearly variations in rainfall and temperatures, makes the right choice of parental genotypes difficult for breeders.

On the other hand, high tillering capacity is recognized to be a good criterion in semiarid environments, where genotypes with high tillering and less variability in number of tillers have been demonstrated to produce high grain yields (Ramos et al., 1982; Hadjichristodoulou, 1985). Nevertheless, tillers may contribute negatively or positively to wheat productivity, depending on the availability of resources such as water, nutrients, and light. The Mediterranean region generally undergoes frequent drought-stress episodes during the vegetative and reproductive periods of the crop cycle. Many of developmental and physiological processes occurring during these periods are subjected to water stress. Genotypes with high tillering capacity usually produce nonsurviving tillers, which transpire limited water resources (Jones and Kirby, 1977; Duggan et al., 2000). This may affect plant growth and production, depending on many variables, such as the duration and severity of stress, the vegetative status of the crop, and the occurrence of other environmental stresses (i.e. light, temperature). Similarly, restricting water availability during anthesis or grain set processes could affect grain weight by inhibiting the translocation of assimilates from the vegetative plant parts to the spikes (Wang et al., 2005), and therefore reduce grain yield. Whereas environments with ample water, as is the case in Northern European countries or under well-irrigated crops, the level of competition in each individual plant with respect to the others is low, allowing plants to produce more fertile tillers contributing to higher yields.

Little is known about differences in tillering habit among wheat genotypes or the contribution of tillers to grain yield in different environments, especially regarding durum wheat under Mediterranean conditions. A good understanding of the contribution of the main stem (MS) and tillers to grain yield may help in the selection of adapted and highly productive new genotypes.

Based on physiological criteria for which the genotypes were selected for this study (García del Moral et al., 2005), we hypothesized that the genotypes with limited tillering may be more beneficial for yield than those with high capacity for tillering under rainfed environments. This paper examines the final grain yield and its components as influenced by MS and tillers, at normal plant density, of 25 durum wheat genotypes under two contrasting water regimes (irrigated and rainfed) in a Mediterranean environment.

2. Materials and methods

2.1. Experimental setup

Four field experiments were conducted in 1996/1997 and 1997/1998 under two water regimes; rainfed (37°10′N, 3°50′W) and irrigated (37°11′N, 3°40′W) in southern Spain. Twenty-five genotypes of durum wheat (*Triticum durum L. var. durum*) were grown in randomized complete-block designs with four replicates in plots of 12 m^2 (six rows, 20 cm apart). At all experimental sites, plant density was adjusted to 350 plants m^{-2}, corresponding to the common plant density in the region. Genotypes consisted of four well-adapted commercial Spanish varieties (Altar-aos, Jabato, Mexa, Vitrón) and 21 genotypes from the CIMMYT/ICARDA durum wheat breeding program (Awalbit, Bicrecham-1, Chacan, Chahra-1, Haurani, Korifla, Krs/Haucan, Lagost-3, Lahn/Haucan, Massara-1, Moulchahba-1, Mousabil-2, Omlahn-3, Omrabi-3, Omruf-3, Quadalete/Erp/Mal, Sebah, Stojocri-3, Waha, Zeina-1, and Zeina-2). These genotypes were selected to represent a wide range of genetic variability based on yield performance and other agronomic criteria (García del Moral et al., 2005). However, the period between planting and heading date for all the genotypes studied was quite similar with slight variations, in order to avoid potential interference of phenology on grain yield and its components.

All plots were weed-free and received adequate fertilizer. Basic fertilization consisted of a mixture of NPK (15:15:15) applied in the seed bed and top dressed ammonium nitro sulphate (26% N). Taking into consideration the soil characteristics of each site, during the first year total fertilization in kg/ha was: 60 + 60 N, 60 P, and 60 K and 45 + 20 N, 45 P, and 45 K in irrigated and rainfed sites, respectively. During the second year the same fertilization was applied at the rainfed site and 60 + 20 N, 60 P, and 60 K in the irrigated one. Irrigation consisted of a total of 150 mm for each year supplied at two different times: 75 mm at the end of the tillering period and 75 mm at the middle of the jointing period.

2.2. Field and laboratory measurements

At the beginning of tillering, five representative plants were sampled at approximately two-week intervals, within a 0.5 m length of central rows, to determine the crop phenology according to Zadoks's scale (Zadoks et al., 1974). At the end of tillering, the maximum tiller number was determined for each plot to estimate the tillering capacity for each genotype. Tiller survival was calculated by dividing the tiller number at harvest by the maximum tiller number present at the end of tillering, expressed as a percentage.

At ripening before grain harvest, plants within 1 m length in a central row of each plot were sampled to measure yield components. The number of plants and spikes per square meter were determined for each plot. Ten representative plants were randomly chosen, and the number of spikes per plant was counted. From these data, the final number of spikes per square meter was estimated and the grain weight per plant was measured. The following yield components were determined separately for MS and tillers: number of spikelets per spike, number of grains per spike, grain weight per spike, and spike length (measured from the collar to the upper spikelet without considering the awns). The number of grains per spikelet was calculated by dividing the number of grains per spike by the number of spikelets per spike. Grain yield and thousand kernel weight (TKW) were recorded separately for the MS and tillers. Moreover, a weighted average per plant was calculated for the number of spikelets per spike, number of grains per spikelet and number of grains per spike.

Grain yield was determined on the basis of the harvested plot in all trials and corrected to a 12% moisture basis. The contribution of MS or tillers of a genotype to total plant yield was determined by dividing the tillers or MS yield of each genotype by the calculated total-plant grain weight, expressed as a percentage.

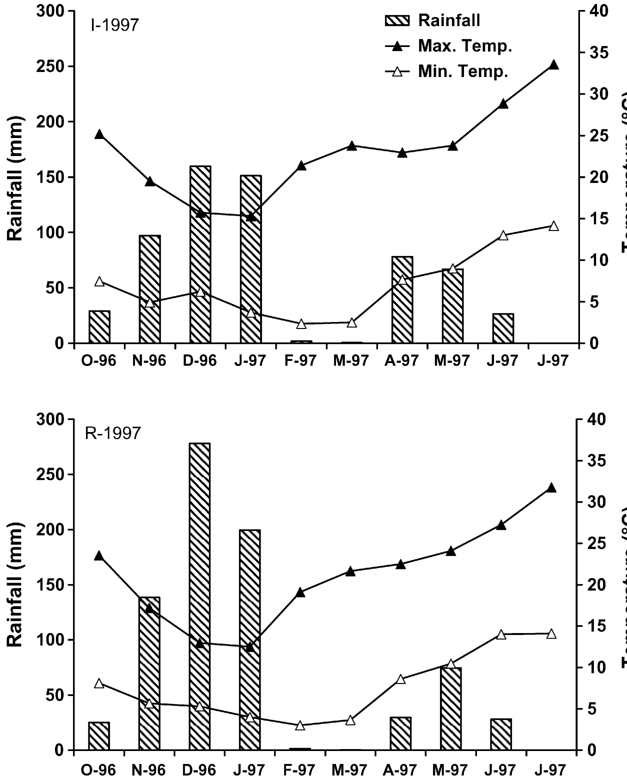

Fig. 1. Rainfall, minimum and maximum temperatures recorded during 1996–1997 in irrigated (I) and rainfed (R) sites.

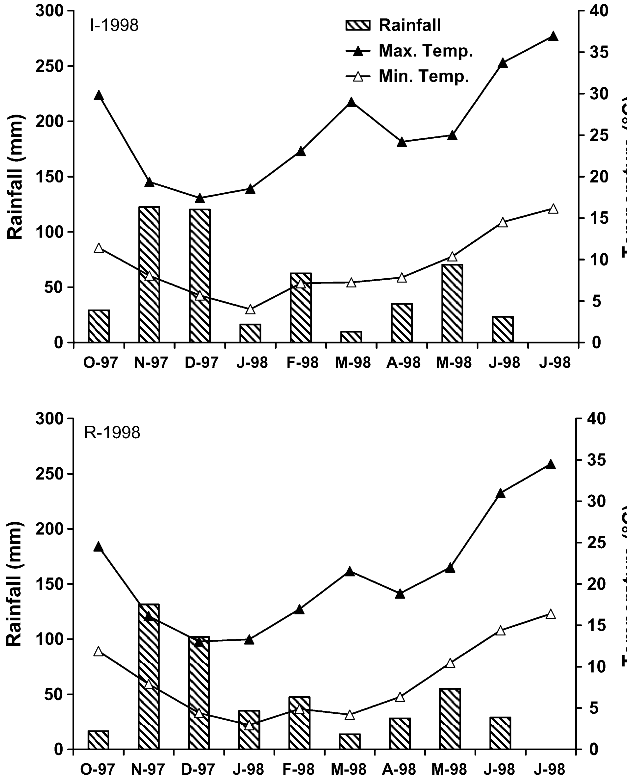

Fig. 2. Rainfall, minimum and maximum temperatures recorded during 1997–1998 in irrigated (I) and rainfed (R) sites.

2.3. Climatic conditions

The climate in the study area is Continental Mediterranean with cold winters and hot summers. Rainfall and minimum and maximum temperatures are shown in Figs. 1 and 2 for the first and second growing seasons, respectively. The seasonal rainfall from sowing to harvesting during the first season was 197 mm at the irrigated site and 184 mm at the rainfed one. Precipitation during winter was adequate, although it was low during two successive months (February and March) with total precipitation no more than 2 mm at both sites (Fig. 1). Temperatures were moderate throughout the growing season in both environments. Average temperatures during grain filling ranged from 8.8 to 23.9 °C and from 11.1 to 23.6 °C at irrigated and rainfed sites, respectively. During the second growing season, total precipitation after planting was higher than in the first

Table 1

Mean values of the whole plant, main-stem, and tiller grain yields, primary yield components, maximum tiller number, and tiller survival of 25 durum wheat genotypes grown over two years (1997 and 1998) under irrigated and rainfed conditions

		Grain yield (kg/ha)	Grain yield per plant (g)	Grains per spikelet	Spikelets per spike	Grains per spike	TKW (g)	Spike length (cm)	Spikes (m^{-2})	Spikes per plant	Max. tiller number (m^{-2})	Tillers survival (%)
Whole plant												
Irrigated	1997	2268	2.2	1.98	11.5	23	37.7	–	497	2.6	1014	52
	1998	4420	3.2	2.05	16.0	32	46.4	–	526	2.1	999	54
Rainfed	1997	1901	1.7	2.36	10.8	25	42.3	–	421	1.5	438	96
	1998	2104	1.3	1.74	11.4	20	40.1	–	471	1.5	620	77
L.S.D.[a]		92	0.1	0.03	0.2	0.8	0.4	–	11	0.1	24	1.8
Main stem												
Irrigated	1997	–	1.8	2.3	13.0	30.7	40.4	5.5	–	–	–	–
	1998	–	2.9	2.3	17.8	41.5	50.2	6.6	–	–	–	–
Rainfed	1997	–	1.9	2.6	12.2	32.1	43.7	4.8	–	–	–	–
	1998	–	1.0	1.9	12.1	23.1	41.9	4.8	–	–	–	–
L.S.D.[a]	–	0.06	0.06	0.2	1	1.0	0.08	–	–	–	–	
Tillers												
Irrigated	1997	–	0.8	1.6	10.5	17.4	30.0	4.6	–	–	–	–
	1998	–	1.4	1.7	14.3	23.8	39.5	5.4	–	–	–	–
Rainfed	1997	–	0.4	0.9	7.4	7.0	21.3	3.3	–	–	–	–
	1998	–	0.7	1.3	9.9	12.9	34.5	4.0	–	–	–	–
L.S.D.[a]	–	0.05	0.08	0.3	1.0	1.5	0.09	–	–	–	–	

[a] Least significant difference at $P = 0.05$.

Table 2
Mean squares from the combined analysis of variance of grain yields, primary yield components, maximum tiller number, and tiller survival of 25 durum wheat genotypes grown over two years (1997 and 1998) under irrigated and rainfed conditions

Source of variation	D.f.	Grain yield ($\times 10^5$) (kg/ha)	Grain yield per plant (g)	Spikes (m^{-2}) ($\times 10^3$)	Spikes per plant	Grains per spike	TKW (g)	Maximum tiller number ($\times 10^4$) (m^{-2})	Tillers survival ($\times 10^2$) (%)
Env[a] (E)	1	2374.7***	140.4***	428.0***	75.0***	2568.9***	69.9***	2275.0***	1124.0***
Year (Y)	1	955.4	7.3	155.7	6.4	428.3	1072.5	70.0	65.9
E × Y	1	600.7***	50.2***	12.4	7.4***	5198.0***	2945.2***	97.2**	119.9***
Gen[a] (G)	24	12.7***	0.9***	14.2***	0.6***	99.6***	155.3***	6.4***	3.4***
G × E	24	4.6**	0.3***	9.6***	0.1	36.9**	20.0***	5.4***	2.5***
G × Y	24	7.1	0.6*	11.8	0.5*	34.6	23.3	7.4	2.6
G × E × Y	24	7.2***	0.3**	8.4***	0.2**	52.0***	13.5***	6.5***	2.2***
Block (E × Y)	12	24.7***	0.3*	16.4***	0.3***	29.5	10.7**	3.4**	2.5***
Error	288	2.2	0.1	3.1	0.1	17.4	3.7	1.5	0.8
Total	399								

*Significant at 0.05 of probability level; **Significant at 0.01 of probability level; ***Significant at 0.001 of probability level.

[a] Env, environment; Gen, genotype.

season, and was more evenly distributed with moderate rainfall during February and March (Fig. 2). The total precipitation was 311 mm at the irrigated site and 288 mm at the rainfed one. Most precipitation occurred after planting, allowing favorable growth conditions. During tillering the temperatures were similar in both environments. However, they were slightly higher at the rainfed site during the grain-filling period. The average temperatures ranged from 12.4 to 26 °C at the irrigated site, and from 13.8 to 28.9 °C at the rainfed one. Between rainfed and irrigated sites, there were no significant differences in either rainfall or temperature, although the total amount of water received at the irrigated sites was greater.

2.4. Statistical analysis

Data were analysed by using the Statgraphics Plus (Version 5.0, Statistical Graphics Corp.). Combined analyses of variance of trials, using the general linear model procedure, were carried out after verifying the homogeneity of trial variance errors using Bartlett's test. Years and replications (blocks) were considered random factors and the remainder effects fixed. Comparisons within the factors were performed by a multiple-range test using the LSD test.

3. Results

3.1. Yield and its components

The average grain yield per area, per plant and the three primary yield components are listed in Table 1. As expected, grain yields (ha^{-1} and $plant^{-1}$) and all yield components were significantly higher under irrigated conditions. On the average, the water supply increased yield by 67% ha^{-1} and by 80% $plant^{-1}$. In the second growing season – characterized by high and good distribution of rainfall – grain yield and its components invariably increased under water supply conditions, but the number of spikes per plant decreased. Under rainfed conditions, the increase in grain yield per area was related mainly to the increase in the number of spikes per square meter.

Combined analysis of variance (Table 2) showed that grain yield per area, yield per plant, number of spikes per square meter, and number of spikes per plant were determined mainly by the water regime, while grains per spike and TKW were influenced largely by environment × year interaction (E × Y). Genotype (G) and its interaction effects were small, even though significantly higher.

Maximum tiller number and tiller survival showed strong variations caused mainly by the environment (Table 1). Irrigation greatly increased the maximum tiller number by 90%, but tiller survival was reduced to 37%. This was deduced also from the combined analysis of variance, as shown in Table 2. Maximum tiller number and tiller survival were primarily influenced by the environment, followed to a lesser degree by the E × Y and year effects. The genotype and its interaction effects were also of small magnitude, although highly significant. Year-to-year climatic fluctuations did not significantly change tillering capacity under irrigated conditions. Tiller survival was slightly different between the two years. However, under rainfed conditions and during the second growing season, tillering increased by 42% but tiller survival declined 20%.

Under irrigated conditions, the genotypes studied showed significant differences in their tillering capacity. The maximum number of tillers per plant varied from 2.2 to 3.5. However, under rainfed conditions theses differences were not significant, the maximum number of tillers per plant ranged from 1.3 to 1.8.

3.2. The effects on main stem and tillers

There was a general reduction in yield and all yield components of MS due to limiting water at rainfed sites, as the average the MS grain yield fell to 38%. Between the two years, MS yield increased by 61% under water supply and in the more favorable season. Almost all yield components increased during this year, except for the number of grains per spikelet, which remained constant (Table 1). However, under rainfed conditions, although the climatic conditions were relatively better in the second year, MS yield decreased (−53%), as did all its components.

The combined analysis of variance (Table 3) shows that the MS yield was determined basically by the E × Y and to a lesser extent by the environment, whereas the number of spikelets per spike and spike length were determined mainly by the effect of the environment, followed by the effect of E × Y. The number of grains per spikelet was determined by the year and E × Y interaction. The TKW was determined mainly by E × Y and to a lesser degree by the year. The genotype effect on MS yield and its components, though of small magnitude, was highly significant.

The contribution of MS to grain yield per plant for all the genotypes studied are listed in Table 4. As shown, in irrigated trials, genotypes differed significantly. In both years, MS contributed equally (the average increase was 68%) to total grain yield per plant. Under water-stress conditions, however, the differences among genotypes were not significant. The contribution of MS differed between the two seasons and depended on climatic fluctuations, contributing 85% in the less favorable season and 59% in the more favorable year. The contribution of MS to grain yield per plant ranged from 63 to 74% in irrigated trials. Massara-1 and Quadalete/Erp/Mal were the genotypes with the highest contribution, while the lowest was Bicrecham-1. Even though there were no significant differences among genotypes in the contributions of MS to grain yield per plant in the rainfed environment, the genotypes studied presented large variations and ranged from 65% for Omrabi-3 and Jabato to 80% for Mexa.

Correlations among grain yield per hectare, per plant, yield components, and the MS yield are presented in Table 5. The irrigated and non-irrigated water regimes showed different correlation levels. Thus, grain yield per hectare and grain weight per plant correlated positively with MS yield under irrigated conditions. Under rainfed conditions, however, the correlation was positive with the yield per plant, but not with yield per hectare. In these environments, the MS yield correlated positively with the number of grains per spike and the number of spikelets per spike; the correlation with TKW

Table 3
Mean squares from the combined analysis of variance of main-stem and tiller grain yields, yield components, and spike length of 25 durum wheat genotypes grown over two years (1997 and 1998) under irrigated and rainfed conditions

Source of variation	D.f.	Grain yield (g)	Spikelets per spike	Grains per spikelet	Grains per spike	TKW (g)	Spike length (cm)
Main stem							
Env[a] (E)	1	78.0***	1064.3***	0.5*	7149.3***	615.6***	150.3***
Year (Y)	1	0.6	539.9	13.4	83.1	1561.4	34.9
E × Y	1	106.8***	595.6***	12.7***	9823.2***	3362.0***	23.9***
Gen[a] (G)	24	0.4***	4.5***	0.4***	117.3***	135.4***	1.0***
G × E	24	0.1*	2.4**	0.2*	47.1*	37.2*	0.2
G × Y	24	0.2	2.4	0.1	54.2	41.8	0.8
G × E × Y	24	0.4***	2.6**	0.2***	60.9***	47.2**	0.4***
Block (E × Y)	12	0.2*	3.8***	0.1	36.8	19.4	0.4**
Error	288	0.1	1.2	0.1	26.2	23.6	0.2
Total	399						
Tillers							
Env[a] (E)	1	33.5***	1421.0***	31.2***	11376.7***	4694.6***	185.7***
Year (Y)	1	21.1	995.2	3.7	3796.5***	12810.2	52.9**
E × Y	1	1.5**	44.0*	2.2	6.0	329.6	0.4
Gen[a] (G)	24	0.2***	6.6***	0.5***	87.2***	152.5***	1.0***
G × E	24	0.2***	3.3*	0.5***	58.7**	176.2***	0.3
G × Y	24	0.2*	5.6*	0.5	84.6	138.2	0.7*
G × E × Y	24	0.1*	2.7	0.4**	42.7*	141.4***	0.3
Block (E × Y)	12	0.1*	8.2***	0.6***	66.8**	165.6***	0.8***
Error	288	0.1	1.9	0.2	26.6	57.5	0.2
Total	399						

*Significant at 0.05 of probability level; **Significant at 0.01 of probability level; ***Significant at 0.001 of probability level.

[a] Env, environment; Gen, genotype.

Table 4
Contribution of main stem and tillers to grain yield per plant of 25 durum wheat genotypes grown over two years (1997 and 1998) under irrigated and rainfed conditions

		Irrigated			Rainfed		
		GYP (g)	MS contribution (%)	Tillers contribution (%)	GYP (g)	MS contribution (%)	Tillers contribution (%)
Jabato		3.2 a	66 c–f	34 c–f	1.9 a–b	65 a	35 a
Awalbit		3.2 a	65 d–f	35 d–f	1.7 b–d	74 a	26 a
Altar-aos		3.2 a	64 e–f	36 e–f	1.4 d–f	75 a	25 a
Bicrecham-1		3.0 a–b	63 f	37 f	1.7 b–d	77 a	23 a
Waha		2.9 a–c	70 a–c	30 a–c	2.0 a	69 a	31 a
Zeina-1		2.9 a–d	67 c–f	33 c–f	1.4 d–f	74 a	26 a
Korifla		2.9 a–d	65 d–f	35 d–f	1.3 d–g	75 a	25 a
Omrabi-3		2.9 a–d	69 a–d	31 a–d	1.5 c–e	65 a	35 a
Lahn/Haucan		2.9 a–d	66 c–f	34 c–f	1.5 c–f	73 a	27 a
Chahra-1		2.8 a–e	66 c–f	34 c–f	1.5 c–e	70 a	30 a
Lagost-3		2.8 a–e	73 a–b	27 a–b	1.5 c–e	66 a	34 a
Quadalete/Erp/Mal		2.7 b–e	74 a	26 a	1.5 c–f	73 a	27 a
Mousabil-2		2.7 b–e	66 c–f	34 c–f	1.1 f–g	71 a	29 a
Chacan		2.6 b–e	66 c–f	34 c–f	1.4 d–f	70 a	30 a
Sebah		2.6 b–f	67 c–f	33 c–f	1.6 b–e	75 a	25 a
Stojocri-3		2.6 b–f	68 c–f	32 c–f	1.4 c–f	72 a	28 a
Moulchahba-1		2.6 b–f	68 c–f	32 c–f	1.3 e–g	71 a	29 a
Omruf-3		2.5 c–f	69 b–e	31 b–e	1.7 a–c	71 a	29 a
Omlahn-3		2.5 d–g	69 a–d	31 a–d	1.6 b–e	72 a	28 a
Krs/haucan		2.4 e–h	70 a–c	30 a–c	1.5 c–e	74 a	26 a
Haurani		2.4 e–h	68 b–e	32 b–e	1.0 g	76 a	24 a
Zeina-2		2.4 e–h	69 a–d	31 a–d	1.4 c–f	72 a	28 a
Vitrón		2.2 f–h	67 c–f	33 c–f	1.3 e–g	79 a	21 a
Massara-1		2.1 g–h	74 a	26 a	1.4 c–f	66 a	34 a
Mexa		2.0 h	68 c–e	32 c–e	1.3 e–g	80 a	20 a
Average		2.7	68	32	1.5	72	28
Year	1997	2.2	68 a	32 a	1.7 a	85 a	15 b
	1998	3.2	68 a	32 a	1.3 b	59 b	41 a

GYP, grain yield per plant. a–c, abc; a–d, abcd, etc.: statistical groups ranked according to Duncan test; numbers followed by the same letter within a column do not differ at 0.05 probability level.

was of lower magnitude. Under irrigated conditions, the MS yield was correlated principally with the number of spikelets per spike and TKW, but not with the number of grains per spikelet (Table 5).

Water stress as inferred from seasonal rainfall and irrigation treatment, affected production more severely in tillers than in the MS, and consequently tiller yield decreased dramatically by 50%, and similar reductions appeared in the other yield components (Table 1). Between years, under irrigated conditions, the season with better climate conditions gave an average yield increase of 75% compared with the drier season. The other yield components also significantly increased. Similarly, under rainfed conditions tiller yield showed the same percentage increase in the second year, and all the yield components increased as well (conversely to MS yield and its components).

The results of the combined analysis of variance for tiller yield and components are presented in Table 3. As shown, tiller yield and its components are strongly dependent on environment. The year effect played a secondary role, while the genotype and its interactions had a modest, but still a significant effect.

The mean contribution of tillers to grain yield per plant averaged 32% in irrigated trials in both years. Under rainfed conditions, however, tiller yield differed significantly between the two seasons, again being higher (41%) in the wetter than in the drier year (15%) (Table 4). Under both environmental conditions, the contribution of tillers to grain yield per plant was substantially lower than that of MS.

Correlations analyses among grain yield per hectare, yield per plant, and yield components of tillers are shown in Table 5. In both environments, the yield per hectare depended mainly on tiller production, while yield per plant depended significantly on the tiller production only under irrigated conditions. Tiller yield under this environment depended mostly on the number of grains per spike, number of spikelets per spike, and TKW. However, under rainfed conditions this parameter depended almost equally on all yield components.

4. Discussion

4.1. Genotype, year, and environment interactions

The high variation in yield found among genotypes, ranging from 1433 to 4286 kg/ha, demonstrated their different grain-yield capacities according to climate and environmental conditions. This variation was due, among other causes, to the different origins of the genotypes and the diverse characteristics upon which they were selected. However, we found a nonsignificant genotype × year interaction (G × Y) on

Table 5
Simple correlation coefficients among grain yield per hectare, grain yield per plant, main stem or tillers yields, and their yield components of 25 durum wheat genotypes grown over two years (1997 and 1998) under irrigated and rainfed conditions

	Grain yield (kg/ha)	Yield per plant(g)	MS or Tillers yield (g)	TKW (g)	Grains per spikelet	No. spikelets
Main stem						
Irrigated						
Grains per spike	**0.6661**	**0.8406**	**0.8822**	0.4249	**0.5754**	**0.8494**
No. spikelets	**0.7911**	**0.8460**	**0.9359**	**0.7033**	0.0644	–
Grains per spikelet	0.0170	0.2742	0.2278	−0.2642	–	–
TKW (g)	**0.6656**	**0.6815**	**0.7673**	–	–	–
MS yield (g)	**0.7840**	**0.9045**	–	–	–	–
Rainfed						
Grains per spike	−0.1022	**0.8368**	**0.9171**	0.1610	**0.9399**	0.4686
No. spikelets	0.2693	**0.5591**	0.3591	0.3254	0.1467	–
Grains per spikelet	−0.1989	**0.7142**	**0.8809**	0.0525	–	–
TKW (g)	0.2589	**0.4815**	0.4363	–	–	–
MS yield (g)	−0.1597	**0.8441**	–	–	–	–
Tillers						
Irrigated						
Grains per spike	**0.5483**	**0.7998**	**0.8974**	0.4347	**0.7454**	**0.7529**
No. spikelets	**0.7417**	**0.8254**	**0.8652**	**0.6754**	0.3142	–
Grains per spikelet	0.1753	**0.4178**	**0.5821**	0.1358	–	–
TKW (g)	**0.7325**	**0.7320**	**0.7514**	–	–	–
Tillers yield (g)	**0.7180**	**0.9065**	–	–	–	–
Rainfed						
Grains per spike	**0.5485**	−0.0165	**0.9570**	**0.7086**	**0.9071**	**0.6906**
No. spikelets	**0.3699**	−0.2187	**0.7088**	0.4608	0.3538	–
Grains per spikelet	**0.4951**	0.1627	**0.8418**	**0.6637**	–	–
TKW (g)	**0.3829**	−0.1648	**0.8320**	–	–	–
Tillers yield (g)	**0.5298**	−0.0849	–	–	–	–

Correlations in bold type are statistically significant at $P = 0.05$.

grain yield, reflecting the fact that the genotypes studied performed similarly in both experimental years (Table 2). Nevertheless, grain yield per plant and the number of spikes per plant showed a modest and significant G × Y interaction, presumably due to the differences in dates of growing periods in each experimental year. Grain yield and yield components were strongly determined by water supply. The high yield responsiveness of the genotypes, registered in the second year, was due mainly to the amount of water received as well as to the good distribution of rainfall during crop growth (Fig. 2).

4.2. Yield per plant and per area

Higher yield per plant under irrigated conditions was determined by tillers as well as MS. Meanwhile, under rainfed conditions, characterized by water shortage and high temperatures, the grain yield per plant was determined mainly by the contribution of MS, especially in the dry year (Table 4). This was probably due to the reduced tillering caused by drought or to a greater potential of MS to contribute to yield when competition for resources is high (Power and Alessi, 1978; McMaster et al., 1994). These results agree with those reported by Moragues et al. (2006) in that durum wheat genotypes that evolved in areas with cold and wet climates produce more tillers than those that evolved in warmer and drier regions. Although the yield per plant was associated with MS production under rainfed regime, the yield on an area basis was determined by tillers rather than MS. In other words, the yield per hectare was determined by the number of fertile spikes (Bauer, 1980; Black, 1982).

4.3. Tillers and MS yield components

The results indicated that tiller grain yield was strongly associated with almost all yield components regardless of the environment (Table 5). However, the yield of MS showed a differential response to the water regime. Water availability during the vegetative and grain-filling stages promoted a close association of yield with the number of spikelets, number of grains per spike and TKW (Table 5). Under rainfed conditions, however, the grain yield was strongly associated with the number of grains per spike. The number of spikelets and TKW were not significantly correlated with grain yield. Spikelet number is determined early in development, after leaf initiation (Kirby and Appleyard, 1984), and water deficit during this stage may result in the death of the distal and basal florets of the spikes (Oosterhuis and Cartwright, 1983). The number of grains per spike is determined later, during tillering and just before anthesis, and therefore unfavorable conditions during this stage mainly affect the number of grains per spike. If water deficit occurs after the flowering stage it reduces kernel weight (Ceccarelli, 1987). The nonsignificant relationship between TKW and grain yield under rainfed conditions, was probably due to the water stress after the flowering stage or in particular during grain filling. However, a significant relationship was found between MS yield and TKW under well-watered conditions, possibly due to the availability of water and the potential of MS to use available resources. Under rainfed conditions, this relationship, though very weak for both MS and tillers, was nevertheless statistically significant for the latter. Similar results were reported by del Blanco et al. (2001) and Ozturk and Aydin (2004), who showed positive correlations between TKW and grain yield. However, no association with grain yield was reported (Housley et al., 1982; Bruckner and Frohberg, 1987).

4.4. Impact of tillering on grain yield

Under irrigated conditions, the genotypes characterized by high tillering capacity were Omrabi-3, Altar-aos, Zeina-1, and Waha. These genotypes performed well and were the most productive ones (grain yields exceed 3700 kg/ha) among the 25 genotypes studied. Under rainfed conditions, yield per unit area of these genotypes decreased but did not differ significantly from Mexa (data not shown), which is a commercial cultivar largely cultivated in Spain during the 1980's (because it assures a minimum yield under dry-land conditions). These results revealed that high tillering genotypes might show yield similar to that of genotypes with restricted tillering, assuring minimum yield under water-stress conditions. However, a suitable number of tillers depend on the seeding rate and the environmental conditions.

The good distribution of precipitation during the second growing season failed to increase tillering under irrigation conditions. The stability of tillering under this environment was assured mainly by irrigation rather than rainfall. Even though the surviving tillers scarcely exceeded 50%, the number of spikes per unit area remained higher, contributing to high yield in this environment (Table 1). While under rainfed conditions, the surviving tillers had no significant influence on grain yield, the lack of a relationship between grain yield and tiller survival might be expected, because the latter did not significantly differ among the genotypes studied. Also we found a weak relationship ($r^2 = 0.11$) between grain yield and the maximum number of tillers. Similar results for winter wheat were reported by Shanahan et al. (1985) and for spring wheat by Sharma (1995). These authors showed a nonsignificant correlation of grain yield with maximum tiller number under conditions of drought stress. Furthermore, Shanahan et al. (1985) found that grain yield was related to tiller survival, but also stated that early tiller appearance positively affected grain yield. In the same way, García del Moral et al. (2005) established a mutual relationship between the vegetative period and maximum tiller number. Recently, Berry et al. (2003) concluded from an experiment on winter wheat, that nonsurviving tillers negatively affect yield in most situations by competing for resources with fertile tillers, the effects being more severe in drought situations.

4.5. Ecophysiological aspects

The water lost through transpiration by unproductive tillers may be significant, especially under arid and semiarid conditions (Richards et al., 2002). Moreover, tillers depend on MS reserves during grain filling, a situation that intensifies competition for resources and may restrict growth, and consequently grain yield (Lauer and Simmons, 1985). On the other hand, unproductive tillers may be beneficial for grain yield by acting as a sink for carbohydrates (Lupton and Pinthus, 1969) and storing nutrients (Garnett and Graham, 2005) that could be remobilized for grain filling. Tillers that failed to survive contributed indirectly to grain yield in that photo-assimilates from young tillers may be allocated to the MS. This agrees with results reported by Chafai et al. (1992) in barley using radiocarbon (^{14}C). Nutrients such as N, K, and P may be also absorbed by the surviving tillers. In addition, tillers can help preserve soil water during early developmental stages – when vigour is high – by minimizing direct evaporation from the soil surface (van Oosterom and Acevedo, 1993), but they can increase transpiration by increasing the leaf-area index.

At critical times (i.e. during initiation of spikelet primordia) under water-stress conditions, the number of kernels may be reduced (García del Moral et al., 2003). Although the percentage tiller survival was higher in the rainfed trials, the number of spikes per plant and the spikes per square meter were higher under irrigated conditions, allowing plants in this environment to produce higher yields. The significant year-to-year variations in tiller survival, under dry-land conditions (increase of 42%), reveals that the climate was the determining factor. However, under adequate water supply, the climate contributed weakly, while irrigation during the reproductive development stage was the key factor affecting the number of fertile spikes (García del Moral et al., 2005).

4.6. Agronomic aspects

Tillering provides the opportunity for crop growers to improve their profit by reducing the sowing rate to the economic optimum. However, limiting wheat to one culm would not outweigh the cost for some cultivars. A study by Spink et al. (2000) on winter wheat showed that compensation for reduced population was due to increased tiller number per plant. Therefore, tillering restriction may cause economic losses when the conditions are favorable for grain production. Most of the beneficial effects of detillering reported in the literature occurred under water-stress environments, where restricted tillering minimize competition for water among surviving tillers, allowing plants to produce more and heavier grains per spike. Increasing water availability commonly reduces the positive effects of detillering, even converting it into a negative one. It is difficult to establish a clear limit between these contrasting effects, especially under field conditions, which are subjected to strong climatic variations, particularly rainfall. Our results revealed that the yield of genotypes with high tillering capacity were similar to that of those with restricted tillering, under relative water-stress conditions of our experiments. We suggest that important differences in yield between these two wheat types (high and low capacity of tillering) under severe drought conditions, give advantages to genotypes with restricted tillering. The data available in the literature covers large geographical areas and different cultivars, indicating a complex G × E × Y interaction, which could partly explain the controversy found in the literature about the effect of tillering suppression on grain yield. The large amount of data available on climate irregularity, and a good understanding of tillering habit may be valuable tools for crop modellers, and may also be of interest in agronomic management practices to optimize crop yield.

5. Conclusions

Grain yield and its components were found to be heavily influenced by water stress and year-to-year climate variations. Under adequate water supply conditions, grain yield per hectare depended at an equal proportion on MS and tiller production. Under rainfed conditions, however, the grain yield depended primarily on tillers. Similarly, grain yield per plant was determined by both MS and tillers under irrigated conditions; conversely, under water-deficit conditions – characterized by high temperatures and limited tillering – the production per plant was determined mainly by MS grain production.

Competition for limiting resources between tillers and MS, as well as their interaction with the environment at each developmental stage resulted in differential associations of grain yield with its components. Thus, in the irrigated environment, both MS and tiller yields depended on the number of grains per spike, spikelets per spike, and TKW. In the rainfed environment, MS yield depended on the number of grains per spike and grains per spikelet, while smaller grains had less influence on MS yield. However, tiller production depended strongly on all yield components.

Our results reveal that high tillering genotypes showed yields similar to those of genotypes with restricted tillering, assuring minimum yield under water-stress conditions. There was no evidence for either a positive or negative effect of maximum tiller number on grain yield under rainfed conditions. However, a suitable number of tillers depend mainly on the environmental conditions.

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